Except for occasional predation on calves by leopards, there was no predation on Nakuru waterbuck. Females spent most of their time inside territories (along the lake shore and along rivers) where the grass appeared to be greener and lusher than in open grassland further away from water (but no measurements of the nutritionally relevant components were taken). Females also spent more time feeding than did males (Wirtz and Oldekop, in prep.). Forage quality appeared to be the main factor governing the distribution of the females.

The nutritional value of many forage species varies greatly with the available moisture. Ungulates require on average 4–5 % crude protein in their diet, but the crude protein content of grass drops from about 8 % in the wet season to 1–3 % in the dry season (Sinclair 1975; Afolayan and Fafunsho 1978). Large scale migrations of ungulates, e.g. the spectacular migration of wildbeest, seem to be a response to forage quality and quantity. Small scale shifts in habitat utilization of nonmigratory African ungulates, such as those shown by Nakuru waterbuck, are probably an analogous process (Kutilek 1979).

"Choice" may be the wrong word to describe the process regulating the distribution of part of the male population. Territory holders excluded most of the remaining adult males and most of the young males from their territories (Wirtz 1982). Analysis of faeces of waterbuck in Rhodesia (Tomlinson 1980a, 1981) and the time budgets of the Nakuru waterbuck (Wirtz and Oldekop, in prep.) indicate that bachelor males are relegated to nutritionally inferior areas. Probably, only a small portion of the adult male population was actually in the preferred location and the sex differences in habitat use were caused by the action of the territorial males that kept most of the male population out of the areas the females used for foraging. Differential distribution of males and females caused by the territorial behaviour of some of the males has been described for several other antelope species and Jarman and Jarman (1973) suggested that, as a consequence, females benefit by an enhanced resource apportionment which might even lead to an increase in calf production.

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Zusammenfassung

Geschlechtsunterschiede und jahreszeitliche Variation in der Habitatwahl in einer Hochdichte-Population des Wasserbocks (Kobus ellipsiprymnus)

Bei Transekt-Zählungen im Nakuru Nationalpark, Kenya, wurde registriert, wie häufig Wasserböcke *(Kobus ellipsiprymnus)* in den verschiedenen Habitaten gesehen wurden. Wasserböcke wurden signifikant häufiger in offenem flußnahem Wald und in offenem Grasland gesehen als dies bei einer gleichförmigen Verteilung über die vorhandenen Habitate zu erwarten war. Die Habitatnutzungsmuster verschiedener Altersklassen und der beiden Geschlechter waren signifikant voneinander verschieden. Die geringste Überlappung in der Habitatnutzung (85 %) war zwischen adulten Weibchen und jungen Männchen. Die saisonalen Unterschiede korrelierten mit der Regenmenge: bei hohen Niederschlagswerten hielten sich die Wasserböcke häufiger in offenem Grasland auf, bei niedrigen Niederschlagswerten mehr in offenem Buschland.

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Summer food habits and quality of female, kid and subadult Apennine chamois, *Rupicapra pyrenaica ornata* Neumann, 1899 (Artiodactyla, Bovidae)

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Abstract

Investigated the summer diet of a flock of the Apennine chamois comprising females, kids and subadults. Monthly observations were carried out between June and September from 1982 to 1984. The study area consisted of grasslands above the timberline belonging to the *Festuco-Trifolietum thalii* plant community, in the upper Val di Rose (Abruzzo National Park, Italy). Our data were obtained from direct observations of grazing animals and from an analysis of the plants browsed. From June to September about 70 % of the total number of species are grazed. However the composition of the diet shows monthly shifts conditioned by the grassland phenology and the grazing selection. A tentative estimate of the main chemico-nutritional features of the diet suggests that the grazing selection keeps the *Festuco-Trifolietum thalii* suitable to supply a protein-rich and fibre-poor diet during the whole summer.

Introduction

The quality and availability of food, together with security aspects, determine the habitat quality for the chamois (Schröder 1971; Elsner-Schack 1985).

While in the north-eastern chamois populations *(Rupicapra rupicapra)* this fact has been extensively studied (see Lovari 1985 for a review), very little is known on the food ecology of the south western species *(Rupicapra pyrenaica)*.

In this paper we give some detailed data on the summer diet of females, kids and subadults of the Apennine subspecies of the south western chamois (*Rupicapra pyrenaica ornata;* Nascetti et al. 1985).

The only remaining population of this subspecies can be found in some mountains in the central Apennines of the Abruzzo National Park (Italy). Holocene remains and historical sources demonstrate a wider range in the central and southern Apennines up to historical times (Masini 1985).

As for studies on the diet of the alpine chamois (e.g. Onderscheka 1974; Dunant 1977; Schröder 1977) and of the Pyrenean one (Berducou 1975; Garcia-Gonzales 1984) these data will provide a background towards clarifying the environmental requirements of this "vulnerable" ungulate (Thornback 1980) and towards ensuring the success of possible reintroductions.

Study area and methods

The study area lies in the upper Val di Rose (Abruzzo National Park, Italy), between Mount Sterpalto (1966 m) and Mount Boccanera (1982 m). This area is part of the Camosciara mountains which are the core of the chamois range in the National Park. Breaches formed by white and grey Dolomitic limestones dating from the Lias characterize the landscape (Praturlon 1968). A mixed beach forest covers the slopes of the mountains up to about the timberline (1700–1800). According to the

phytosociological approach (Braun-Blanquet 1964) the alpine grasslands belong to the vegetation types *Festuco-Trifolietum thalii* and *Avena versicolor-Koeleria splendens* community. Only the former is intensively grazed in summer by flocks of females, kids and subadults; the latter is grazed by solitary adult males. We therefore concentrated our observations on the *Festuco-Trifolietum thalii*. The plant community was sampled with the phytosociological method (Braun-Blanquet 1964) and the cover of the species was estimated in a simplified way as 3: beyond 2/3, 2: from 1/3 to 2/3; 1 up to 1/3 of the minimal area of the relevé. The sampling of the grazed species was carried out by direct observations. Our data were collected monthly for three years (1982 to 1984), from June to September, except for August (1983). The seasonal period we considered corresponds at first to the lactation and then (August-September) to the early weaning of kids. The flocks were observed using 12 × 50 binoculars from a distance of about 30–40 m. For each of the grazed species, the parts of the plant were noted (F: flowers; L: leaves; Fr: fruits), and the average grazing frequency (g.f.) was estimated (3: beyond 2/3; 2: from 1/3 to 2/3; 1: up to 1/3), using a slight modification of the scale proposed by Dunant (1977). Nomenclature of taxa follows Pignatti (1982), except for *Graminaceae* (Tutin et al. 1964–80). A tentative estimate of the chemical composition of the diet was carried out by analysing 100 g samples of the monthly diet. The grazed parts of the plants were weighted on the basis of species cover in the phytosociological relevés. For each species and each month the calculation was as follows:

$$\text{Grazed part weight (g)} = \frac{\text{Part grazing frequency} \times \text{species cover}}{\text{Total grazing frequency} \times \text{Total species cover}} \cdot 100$$

The values we have considered in the calculation are in Table 1. Samples were weighed on a digital portable balance. They were sealed under vacuum in plastic containers and maintained at 0 °C until analysing.

The samples were dried in a forced ventilation heater at a temperature of 65 °C up to constant weight. The content of crude protein, calcium, phosphorus, magnesium (A.O.A.C. 1984) and cell wall constituents (NDF; Goering and Van Soest 1970) were determined.

Results

The specific composition and phenology of diet

The sampled species are listed in Table 1. There are 54 grazed species; the total number of species is 78. This means that, during the observation period, the flocks grazed 69.2 per cent of the total number of species.

The specific composition of the grasslands is that of the vegetation type *Festuco-Trifolietum thalii*, here characterized by *Festuca violacea macrathera, Trifolium thalii, Crepis aurea glabrescens* and *Plantago atrata*.

Considering as available only those species which, in each month, were at phenological phases unlike "seedling" or "dried plant", we can see (Fig. 1) that the number of available species is lowest in June, and is almost constant from July to September. Ratios between grazed species and available species show no significant differences during the whole summer.

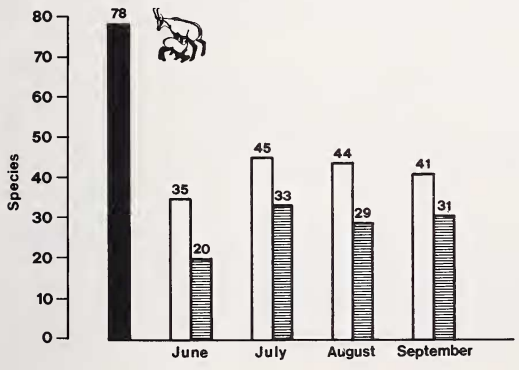

Fig. 1. Number of grazed species (striped column) during the summer in relation to the total number of species (black column) and the available species (white column). Monthly ratios between grazed and available species are the following: June: 0.57; July: 0.73; August: 0.66; September: 0.76. Grazed species are listed in Table 1; available species in Table 2. (Further explanations in the text)

Table 1. **Festuco-Trifolietum thalii**
Grazed species

Species	June		July		Aug.		Sept.	
	F	L	F	L	F	L	F-Fr	L
Aspidiaceae								
Polystichum lonchitis (1)		3		3				
Campanulaceae								
Phyteuma orbiculare (1)			1					
Chenopodiaceae								
Chenopodium bonus-henricus (1)			2	2	2	2	2	2
Compositae								
Achillea millefolium (1)					1			
Adenostyles australis (1)			3	3				
Aster bellidiastrum (2)	3	3	2					2
Bellis pusilla (1)	3	3	2	2		2		3
Carduus carlinaefolius (1)			1	1				
Chrysanthemum tridactylites (1)			2	2				
Cirisum eriophorum (1)			1				2	
Crepis aurea glabrescens (3)		2	3	3		2	3	3
Doronicum columnae (1)	3		3			1		2
Leontodon hispidus (1)								1
Senecio rupestris (1)			1				1	
Taraxacum officinale (2)		2	2	3	3			
Cruciferae								
Arabis alpina caucasica (1)			1	1				
Cupressaceae								
Juniperus nana (1)		2						
Gentianaceae								
Gentiana lutea (1)		3		2		3		
Geraniaceae								
Geranium cinereum (1)								3
Geranium macrorrhizum (1)								3
Graminaceae								
Festuca dimorpha (1)						3		
Festuca nigrescens (1)	3	3	2			2		2
Festuca robustifolia (1)	3	3				3		2
Festuca violacea macrathera (2)		3		1		3		
Phleum alpinum (1)						1		
Poa alpina (2)	2	2	2	2		2		
Juncaceae								
Luzula sieberi (2)						3	2	2
Leguminosae								
Anthyllis vulneraria group (1)			2					
Astragalus depressus (1)							2	2
Medicago lupulina (1)						1		
Trifolium pratense semipurpureum (1)	1			2	1	1	2	2
Trifolium repens (1)							2	2
Trifolium thalii (3)	2	2	3			3	3	3
Liliaceae								
Veratrum album lobelianun (1)			2	2		3		1
Orobanchaceae								
Orobanche sp. (1)							1	1
Plantaginaceae								
Plantago atrata (3)	3	3	2	2		3		3
Plumbaginaceae								
Armeria majellensis (1)			1			2		2
Polygonaceae								
Rumex acetosa (2)	3		3	3			3	3
Primulaceae								
Soldanella alpina (1)						2	1	1

Table 1 (continued)

Species	June		July		Aug.		Sept.	
	F	L	F	L	F	L	F-Fr	L
Ranunculaceae								
Pulsatilla alpina alpina (1)					3	3		
Ranunculus apenninus (2)	2	2	1			2	2	2
Rubiaceae								
Galium anisophyllum (1)			1					
Scrophulariaceae								
Linaria purpurea (1)							1	
Pedicularis comosa (1)						3		
Rhinanthus alectorolophus (1)					1	1	1	1
Scrophularia scopolii (1)	1	1			1			
Verbascum longifolium (1)		1						2
Thymelaeaceae								
Daphne mezereum (1)							1	2
Umbelliferae								
Chaerophyllum hirsutum hirsutum (1)			1	1	3	3		
Chaerophyllum hirsutum magellense (1)			1	1		3		
Heracleum pyrenaicum orsini (2)		3	3	3		3	2	2
Pimpinella alpestris (1)			3	3				
Valerianaceae								
Valeriana montana (2)			3				3	
Violaceae								
Viola eugeniae eugeniae (1)			1				1	

Mean cover (within brackets): 1 = up to ⅓; 2 = from ⅓ to ⅔; 3 = beyond ⅔. Grazed parts: F = flowers; L = leaves; Fr = fruits. Grazing frequencies: 1 = up to ⅓; 2 = from ⅓ to ⅔; 3 = beyond ⅔. Further explanations in the text.

Table 2. ***Festuco-Trifolietum thalii***

Available ungrazed species in each month

June (15)	Compositae: *Gnaphalium diminutum, Chrysanthemum tridactylites, Senecio rupestris, Taraxacum officinale*; Cruciferae: *Erysimum majellensis*; Gentianaceae: *Gentiana nivalis*; Labiatae: *Stachys alopecurus divulsa; Thymus serpyllum* group; Plumbaginaceae: *Armeria majellensis*; Primulaceae: *Soldanella alpina*; Ranunculaceae: *Pulsatilla alpina*; Rosaceae: *Alchemilla nitida*; Rubiaceae: *Galium anisophyllum*; Scrophulariaceae: *Scrophularia scopolii*; Umbelliferae: *Pimpinella alpestris*.
July (12)	Boraginaceae: *Myosotis alpestris*; Compositae: *Achillea millefolium, Carduus chrysacanthus*; Cupressaceae: *Juniperus nana*; Geraniaceae: *Geranium cinereum, Geranium macrorrhizum*; Labiatae: *Lamium maculatum, Thymus serpyllum* group; Primulaceae: *Soldanella alpina*; Rosaceae: *Alchemilla nitida*; Scrophulariaceae: *Scrophularia scopolii, Verbascum longifolium*.
August (15)	Aspidiaceae: *Polystichum lonchitis*; Campanulaceae: *Campanula scheuchzeri*; Caryophyllaceae: *Cerastium tomentosum*; Convolvulaceae: *Cuscuta* sp.; Cupressaceae: *Juniperus nana*; Cyperaceae: *Carex kitaibeliana*; Graminaceae: *Dactylis glomerata, Bromus erectus*; Labiatae: *Thymus serpyllum* group; Rubiaceae: *Asperula aristata, Galium anisophyllum*; Scrophulariaceae: *Linaria purpurea, Verbascum longifolium*; Umbelliferae: *Seseli libanotis*; Urticaceae: *Urtica dioica*.
September (10)	Aspidiaceae: *Polystichum lonchitis*; Caryophyllaceae: *Cerastium tomentosum*; Compositae: *Achillea millefolium, Carduus chrysacanthus, Taraxacum officinale*; Cupressaceae: *Juniperus nana*; Juncaceae: *Juncus monanthos*; Labiatae: *Stachys tymphaea*; Santalaceae: *Thesium parnassi*; Urticaceae: *Urtica dioica*.

Nevertheless, if we compare two by two the monthly lists of grazed species (Table 1) through their common species and their species restricted to one month, we can see that the floristic composition of the diet shows a significant difference between June and July ($\chi^2 = 3.94$ with 1 df, and significant at $P = 0.05$).

In Table 1 we also can see that: only the flowers of the species *Phyteuma orbiculare, Achillea millefolium, Cirsium eriophorum, Senecio rupestris, Anthyllis vulneraria* group, *Galium anisophyllum, Linaria purpurea, Valeriana montana, Viola eugeniae* subsp. *eugeniae* are eaten. 9 species altogether.

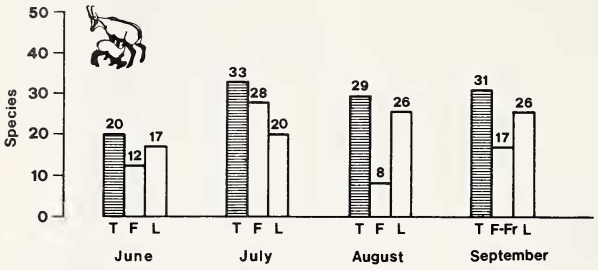

Fig. 2. Number of grazed species (T) subdivided according to parts eaten. F = flowers; Fr = fruits; L = leaves

Only the leaves are grazed in the following species: *Polystichum lonchitis, Gentiana lutea, Geranium macrorrhizum, Festuca dimorpha, Festuca violacea* subsp. *macrathera, Phleum alpinum, Medicago lupulina, Juniperus nana, Pedicularis comosa, Verbascum longifolium, Daphne mezereum*. 11 species in all.

The other grazed species (34) are subjected to an indiscriminate form of grazing.

Fig. 2 shows that in July there is a clear preference for flowers. From July to August there is a marked decrease in the grazing of flowers. ($\chi^2 = 18.50$ with 1 df, highly significant). Leaves are grazed with high frequency during the whole observation period.

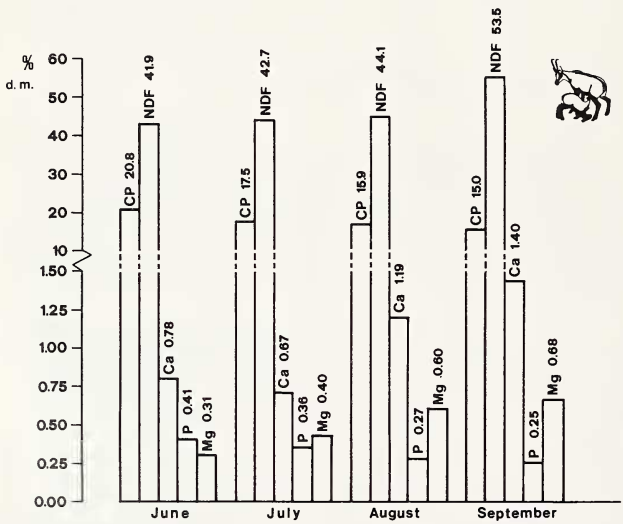

Fig. 3. The main chemico-nutritional features of the summer diet. Monthly per cent content on the dried matter (d. m.) of crude protein (CP), cell wall constituents (NDF: neutral detergent fiber) and some elements. (Further explanations in the text)

The main chemico-nutritional features of the diet

Fig. 3 shows the results of our tentative estimate of some chemico-nutritional features of the diet. The differences between our monthly data have no statistical significance. However, their apparent trends suggest a decrease in the crude protein (CP) and phosphorus content of the diet and an increase in cell wall constituents (NDF), calcium and magnesium, from June to September.

Discussion

The grassland grazed in summer by females, kids and subadults of the Apennine chamois belong to a vegetation type *(Festuco-Trifolietum thalii)* which is common in the alpine vegetation belt of the Alps, but is rare and extrazonal in the high mountains of northern and central Apennines (Pignatti 1979). Some significant subspecies such as *Festuca violacea* subsp. *macrathera* and *Crepis aurea* subsp. *glabrescens* indicate a slight chorological difference between the Apennine community and the *Festuco-Trifolietum* described for the Alps (Braun-Blanquet 1949–50). As in the Alps its distribution is restricted to sites with a long-lasting snow covering and weakly acid soils. In the Abruzzo National Park, such environmental conditions occur in some northern slopes of the Camosciara mountains – which include the upper Val di Rose – but are rare and fragmentary elsewhere, as, for instance, on Mount Amaro (1862 m). The striking difference between the great number of chamois in the Camosciara with respect to other Park areas could be explained on the basis of the importance of the *Festuco-Trifolietum thalii* as a food source especially during lactation. The phenology of this plant community has a role in determining the grazing habits of females and subadults and some nutritional shifts in the diet.

From June to September the increase of magnesium (from leaves) and the decrease of phosphorus (from flowers), as our data indicate, are well known phenologically related facts.

The high values found in June in the phosphorus content of the diet (0.42 % of the d. m.) may be related to the corresponding chamois preference for the floral parts of plants. Moreover, it is well known that grasses and many other plants show decreasing phosphorus contents evolving from the early stage (0.40 % of the d. m.) to the end of flowering (0.20 % of the d. m.; Bouquet and Guegen 1979).

On the contrary, the phenologic decrease of proteins (from young leaves and flowers) corresponds to only an apparent slight decrease of protein content in the diet. As suggested by Fig. 4, this fact may be well explained on the basis of an increasing grazing frequency of Leguminosae leaves from June to September. The proteins of these leaves have a high digestibility and exercise a stimulating effect on the rumination (Grenet and Demarquilly 1977). In *Trifolium repens* Ulyatt (1981) observed a good digestibility even in an advanced vegetative state, as the herbivores only graze the leaves and the leafstalks of this clover. This removal should provoke a regeneration of a new leaf tissue which would keep up the supply of low fibre content forage but with high protein content.

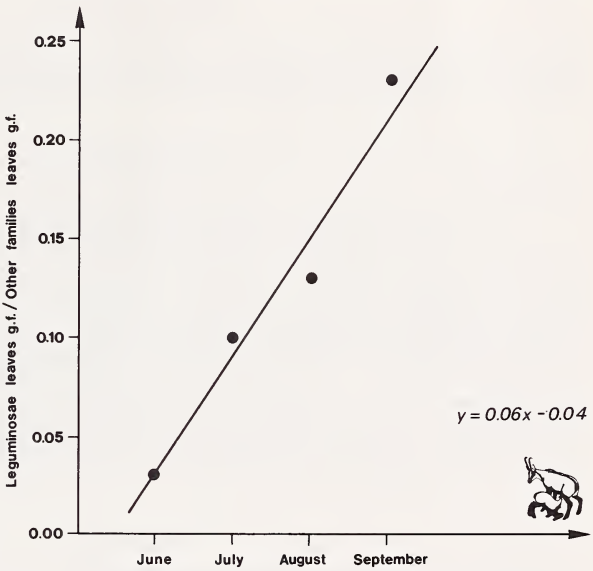

Fig. 4. Monthly ratios between the grazing frequency of Leguminosae leaves and the grazing frequency of leaves of other families. Grazing frequencies (g. f.) are estimated according to Dunant (1977), modified. June: 0.03; July: 0.10; August: 0.13; September: 0.23. The correlation coefficient r = 0.98, with 1 df, is highly significant